

## OBSERVATIONS ON THE NESTING BIOLOGY AND BEHAVIOR OF *TRYPOXYLON (TRYPARGILUM) VAGULUM* (HYMENOPTERA: SPHECIDAE) IN COSTA RICA

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*Abstract.*—*Trypoxylon (Trypargilum) vagulum* Richards, a spider-hunting sphecid wasp, was studied at the Organization for Tropical Studies' field station at La Selva in Costa Rica. The wasps constructed nests in trap-nests with tube diameters of 3.2, 4.8, and rarely 6.4 mm. Nest structure, cocoon morphology, and differences between male and female provisions are discussed. Brood cells were provisioned with 7 to 35 spiders comprised mostly of juvenile snare-building spiders of the families Araneidae, Tetragnathidae, Theridiidae, and Uloboridae. Prey also included a few juvenile Clubionidae, Ctenidae, and Pisauridae. Natural enemies were *Lepidophora trypoxylona* Hall (Diptera: Bombyliidae), *Amobia erythura* (Wulp) (Diptera: Sarcophagidae), *Phalacrotophora punctiapex* Borgmeier (Diptera: Phoridae), *Macrosiagon lineare* (Le Conte) (Coleoptera: Rhipiphoridae), *Trichrysis nigropolita* (Bischoff) (Hymenoptera: Chrysididae), and ants (Hymenoptera: Formicidae).

*Key Words.*—Insecta, Hymenoptera, Sphecidae, *Trypoxylon*, Biology, Behavior, Costa Rica.

During 1980 and 1981 we conducted a trap-nest survey in the atlantic lowlands of Costa Rica to obtain comparative biological information on poorly known neotropical species of *Trypoxylon*. Two earlier papers described the nests of *T. (Trypargilum) xanthandrum* Richards (Coville & Griswold 1983) and *T. (Trypargilum) superbum* Smith (Coville & Griswold 1984); both species are uncommon wasps. In this paper we describe the nesting biology and behavior of *T. vagulum* Richards, the most frequently trap-nested wasp or bee in the study.

*Trypoxylon (Trypargilum) vagulum* is a solitary wasp, first described by Richards (1934) from a single male taken at Magdalena, Colombia. The female has only recently been described and the known range of the species shown to extend from Veracruz, Mexico, to Colombia (Coville 1982). Its biology is poorly known. Rau (1933, 1935) reported that *T. vagulum* built its larval cells within old mud cells from nests of *T. (Trypoxylon) fabricator* Smith. Griswold & Coville (1986), using a sample of spider prey from nests of *T. vagulum* built in trap-nests, examined the diurnal habits of the types of spiders taken.

### STUDY SITE

The trap-nest study conducted in 1980 and 1981 was at La Selva, a field station of the Organization for Tropical Studies, located (84°00–02' W, 10°24–26' N) near the town of Puerto Viejo de Sarapiquí, Heredia Prov. (see Coville & Griswold, 1983, 1984). Nests of *T. vagulum* were obtained in trap-nests in four habitats.

*Successional strips.*—Trap-nests were placed along the edge of newly cut strips that bordered an old cacao plantation in 1980 and lowland tropical rainforest in 1981 (see Coville & Griswold 1983, 1984).

*Arboretum.*—Trap-nests were placed throughout a 3.5 ha area circumscribed

by undisturbed lowland tropical rainforest and an abandoned cacao plantation (see Coville & Griswold 1983: fig. 2). In the arboretum the undergrowth was periodically cleared with machete to provide easy access to numerous trees that possessed identification numbers.

*Rafael's house.*—Coville & Griswold (1984) described this residence. Trap-nests were placed in trees about the yard in 1981 only.

*Living quarters.*—The main structure at La Selva during the study was also the principal nesting area of *T. vagulum* in 1980 and 1981. Trap-nests were attached to beams, railings and other parts of the building.

#### MATERIALS AND METHODS

Coville & Griswold (1983) provide details of the general trap-nest and rearing techniques used in the study. We used three types of trap-nests. Standard trap-nests were  $2 \times 2 \times 16.5$  cm blocks of straight grain pine or fir. An 11.0, 9.5, 8.0, 6.4, or  $4.8 \times 155$  mm hole was drilled in each block. Trap-nests with  $3.2 \times 85$  mm holes drilled in them were made from smaller blocks,  $1 \times 1 \times 10$ – $12$  cm. Short trap-nests had holes 9.5, 6.4, and 4.8 mm drilled to a depth of only 75 mm. Bundles containing one or two trap-nests (either standard or short trap-nests, but not both types) with different sized holes were attached to various objects. Bundles with standard trap-nests were used in all habitats, but bundles with short trap-nests were used only at the living quarters. Each bundle in the field was subsequently examined 1–3 times per week. Bundles at the living quarters were examined daily. During these examinations, we collected trap-nests containing completed wasp nests and replaced them with trap-nests of the same type. This generally ensured that wasps had a choice of trap-nest diameters to use in building nests.

To facilitate behavioral studies, special observation trap-nests were also used at the living quarters. Observation trap-nests had clear or red transparent plastic taped over a U-shaped groove or grooves routed in blocks of wood. The grooves were 9.5, 6.4, 4.8 or 3.2 mm in diameter and their length approximated the depth of the corresponding diameter holes in standard trap-nests. We sectioned standard trap-nests and glued a piece to the front of each observation trap. As a result, the entrance to each observation trap resembled the circular entrance of a standard trap-nest. Another thin piece of wood was lain over the plastic and loosely wired into place. This cover created within the grooves a dark environment necessary to induce the wasps to build their nests. Once a nest had been initiated the cover could be removed so that the wasp's nesting activity could be directly observed. The red plastic caused the least disturbance of the wasps, but was so dark that we had to use a flashlight to clearly observe their activity. Our later observation traps all had clear plastic windows. When making routine observations of the wasp' behavior we laid a piece of red plexiglass on top of the window so as to cause as little disturbance of the wasps as necessary. For detailed observation or photography we would carefully remove the red plexiglass for short periods.

Adult wasps, individual spider prey and the contents of newly provisioned cells were weighed on a Mettler balance. After weighing, cell contents were carefully placed in artificial cells within grooves of certain observation trap-nests for rearing the wasp egg to the adult stage. These rearing traps were stored in a tightly sealed plastic box provided with a few balls of moist cotton to maintain a high humidity.

Table 1. Summary of trap-nest study at La Selva during 1980 and 1981 at locations frequented by *Trypoxylon vagulum*.

Location	No. of trap-nest bundles	Bundle pattern <sup>a</sup>	Date bundles set out	Date study ended	No. of bundles with <i>T. vagulum</i> nests	No. of <i>T. vagulum</i> nests
Successional strips	5	1	9-II-80	5-IV-80	0	0
	10	1	30-VII-80	13-IX-80	6	16
	10	2	4-IX-81	22-X-81	1	1
Arboretum	13-15	1	12/13-IV-80	13-IX-80	8	28
	20	2	3-IX-81	24-X-81	2	8
	4	3	9-IX-81	24-X-81	0	0
Rafael's house	5	3	5-IX-81	22-X-81	2	2
Living quarters	5	1	15-II-80	15-IX-80	5	72
	5	4	6-VIII-80	9/18-IX-80	5	13
	10	4	3-IX-81	26-X-81	8	26
	2	3	7-IX-81	26-X-81	2	10

<sup>a</sup> Patterns 1, 2, and 3 had standard trap-nests; pattern 4 had short trap-nests. In pattern 1 bundles contained one 9.5, two 6.4, two 4.8, and two 3.2 mm diameter trap-nests. In pattern 2 bundles contained two each of 11.0, 9.5, 8.0, 6.4, 4.8, and 3.2 mm diameter trap-nests. In pattern 3 bundles had one each of 11.0, 9.5, 8.0, 6.4, 4.8, and 3.2 mm diameter trap-nests. In pattern 4 bundles had two each of 9.5, 6.4, and 4.8 mm diameter trap-nests.

The box was left outside in a screened enclosure. It was examined once or twice per day to determine how the larvae were developing and to make sure no ants had succeeded in entering the container. Once the larvae had completed their cocoons they were transferred to gelatin capsules, where they remained until emergence.

Voucher specimens of the spider prey are labelled 'Coville & Griswold *Trypoxylon* study' and are deposited at the California Academy of Sciences. Specimens of the wasps are deposited in the Essig Museum of Entomology at the University of California, Berkeley.

## RESULTS

*Trypoxylon vagulum* nested in 176 standard and short trap-nests (Table 1) and accepted trap-nests with 3.2, 4.8, and 6.4 mm diameter holes. In bundles containing equal numbers of all three diameter traps (configurations 1-3 in Table 1), *T. vagulum* showed a greater preference for those with 3.2 mm diameter holes (85) over those with 4.8 (50) and 6.4 (2) mm diameter holes.

We also obtained 10 nests of *T. vagulum* from observation trap-nests; 3 nests were in 4.8 mm diameter grooves and 7 were in 3.2 mm diameter grooves. The discussion on nest characteristics, prey, and enemies pertain to information gathered from the standard and short trap-nests.

Trap-nests set out at the living quarters produced most nests (Table 1). Dwellings and other human structures seem to be a favorable habitat for these wasps, perhaps because they provide numerous suitable nest sites. *Trypoxylon vagulum* readily utilized nail holes and abandoned cells of mud-daubing wasps such as *T. (Trypoxylon) fabricator*. One even built its nest in the handle of one of our spare insect nets. Generally the overhanging roof protected the nest sites from rain.

Table 2. General structural characteristics of 155 completed nests of *Trypoxylon vagulum* in standard and short trap-nests.

	Trap-nest tube sizes in mm		
	4.8 × 155	4.8 × 75	3.2 × 85
Total no. of completed nests	41	36	78
No. of nests:			
With vestibular cells	34	23	47
Without vestibular cells	7	13	31
With intercalary cells	12	4	4
Without intercalary cells	29	32	74
With closure plug at entrance	35	27	72
With recessed plug	6	9	6
With first cells at inner end of tube	36	35	56
With first cells at distance from end of tube	5	1	22
Provisioned cells:			
Total no.	230	159	272
No. of cells per nest			
range	1-10	1-6	1-6
mean ± SD	5.6 ± 2.4	4.4 ± 1.4	3.5 ± 1.5
Average no. of cells per cm of nest tube	0.36	0.59	0.75

Thus trap-nests used at the living quarters were set out in an area with many wasps already nesting. The wasps quickly discovered the trap-nests. At times, 4 pairs of *T. vagulum* were found nesting in a single bundle of trap-nests at the living quarters.

The other sites (Table 1) were more complex environments in which suitable nest sites were more scattered. The wasps were probably more dispersed than at the living quarters and consequently only rarely discovered the trap-nests. Once a female of *T. vagulum* discovered a bundle of trap-nests she would build many successive nests in the same bundle, for as long as suitable diameter traps were available.

*Nest Structure.*—Nests in all diameter tubes were similar. The wasps initiated nests by first depositing a preliminary mud plug. The preliminary plug was usually a small bit of mud placed at the inner end of the trap-nest tube. Occasionally, the preliminary plug was a mud wall or partition placed a variable distance from the inner end (see Table 2). The distance in 4.8 × 155 mm tubes was 26.4–112.0 mm ( $\bar{x}$  = 60.5 mm,  $n$  = 4 of 5 instances reported in Table 2). In one 4.8 × 75 mm tube the distance was 3.0 mm. Finally, in 3.2 × 85 mm tubes the distance was 7.9–45.6 mm ( $\bar{x}$  = 25.8 mm,  $n$  = 12 of 22 instances reported in Table 2).

Following the preliminary plug the wasps usually built a series of brood cells arranged end to end along the length of the trap-nest tube. An empty cell preceded the first brood cell in one nest in a 4.8 × 155 mm trap and 2 nests in 3.2 × 85 mm traps. Two empty cells preceded the first brood cell in one 3.2 × 85 mm trap.

Each brood cell was separated from the neighboring cells by a mud cell partition. The inner surface of the cell partitions were convex with a rough lumpy surface. The outer surfaces were smoothly concave without mud globules ap-

pressed to the surface. The wasps did not line the trap-nest tubes with mud, so the exposed wood lining the tubes formed the lateral walls of the brood cells. Occasionally one or more empty cells (intercalary cells of Krombein 1967b) were placed between adjacent brood cells. Intercalary cells occurred most frequently in  $4.8 \times 155$  mm trap-nests. We are uncertain as to their significance (see discussion by Krombein 1967b). Many nests had one to 4 empty cells (vestibular cells of Krombein 1967b) placed between the last provisioned cell and the mud closure plug that sealed the entrance to completed nests (Table 2). Vestibular cells are commonly found in nests of many kinds of wasps and bees and presumably discourage enemies from penetrating far enough into completed nests to reach the larval cells (see Krombein 1967b).

All completed nests possessed a closure plug (Table 2). In only one case was the closure plug recessed by more than 5 mm (the closure plug was recessed by 15.2 mm in one  $4.8 \times 155$  mm nest). Detailed structure of the closure plug was examined in thirty-nine  $4.8 \times 155$  mm nests, thirty-five  $4.8 \times 75$  mm nests, and seventy-six  $3.2 \times 85$  mm nests (Table 3). Among nests in which the closure plugs were examined, plugs consisted of 1 or 2 mud elements, except one  $4.8 \times 155$  mm nest had 3 elements in its closure plug. Most nests in 4.8 mm diameter tubes had a single element (26 vs. 12 nests in 155 mm tubes and 25 vs. 10 nests in 75 mm tubes). One and two element plugs were found in an equal number of  $3.2 \times 85$  mm nests (38 nests each). The inner elements were similar to cell partitions. The outer element, which was appressed to the inner elements or separated from it by less than 1.0 mm, was generally thicker. When placed at the nest entrances the outer surface of the closure plug was always smooth and flat or only slightly concave. In addition, the plugs were clearly defined in that the mud was not spread onto the wood of the trap-nest.

Small partial mud rings were found in some cells and appeared to represent sites where a female had initiated and then aborted construction of a cell partition. In an observation trap-nest we also observed a female apparently accidentally drop part of the mud she was carrying for constructing a cell partition. This dropped mud remained in the cell. Similar deposits were occasionally found in other trap-nests.

For nests opened after all wasp larvae had formed cocoons we took paired measurements of cell lengths and head widths of the reared wasps (Table 4). The relationship of cell length and wasp size (head width) was determined with Pearson's product moment correlation coefficient ( $r$ ). In 3.2 mm diameter nests among male cells  $r = 0.01$  ( $n = 64$ ) and among female cells  $r = 0.31$  ( $n = 18$ ). In  $4.8 \times 155$  mm nests among male cells  $r = -0.11$  ( $n = 25$ ) and among female cells  $r = -0.17$  ( $n = 40$ ). None of the  $r$  values were significant at  $P < 0.05$ , so we concluded that among wasps of the same sex cell length is not correlated with wasp size.

*Sex ratios and arrangement of male and female cells.*—The effects of nest length and diameter on sex ratios were examined from data presented in Table 5. Nest length in 4.8 mm diameter trap-nests did not have any apparent effect on sex ratios. The proportion of males and females reared from conventional and short trap-nests with tube dimensions of  $4.8 \times 155$  mm and  $4.8 \times 75$  mm, respectively, were not significantly different ( $\chi^2 = 0.32$ ,  $df = 1$ ). Nest diameter did have an effect. Trap-nests with 4.8 mm diameter tubes produced more than 2

Table 3. Dimensions of nests of *Trypoxylon vagulum* in trap-nests (measurements in mm).

	Nest tube diameter × length			
	3.2 × 85	4.8 × 75	4.8 × 155	6.4 × 155
Female cell length <sup>a</sup>				
range	9.4–32.2	9.9–27.9 <sup>b,d</sup>	8.3–27.6 <sup>a,b</sup>	13.2–14.4
mean ( <i>n</i> )	16.4 (19)	12.5 (46)	14.6 (54)	13.8 (3)
Male cell length <sup>a</sup>				
range	9.8–32.9 <sup>a,c</sup>	8.3–19.7 <sup>c,d</sup>	10.6–18.9 <sup>a,c</sup>	—
mean ( <i>n</i> )	16.5 (108)	11.5 (20)	13.0 (28)	—
Vestibular cell length				
range	1.3–53.7	1.4–27.4	2.8–90.4	—
mean ( <i>n</i> )	10.9 (33)	8.9 (12)	22.0 (23)	—
Intercalary cell length				
range	5.0	3.7	5.1–34.8	—
mean ( <i>n</i> )	5.0 (1)	3.7 (1)	20.0 (2)	—
Cell partition thickness				
range	0.4–1.6	0.3–1.4	0.4–0.8	—
mean ( <i>n</i> )	0.7 (27)	0.6 (56)	0.7 (4)	—
Closure plug thickness				
range	0.4–4.3	0.6–3.8	1.4–1.5	—
mean ( <i>n</i> )	2.1 (34)	1.7 (29)	1.5 (2)	—

<sup>a</sup> Measurements do not include brood cells considered abnormally long. For 3.2 and 4.8 mm diameter nests cells greater than 2 standard deviations from the mean for all (male and female) cells were deleted. Deleted cells included 4 male cells (42.7, 43.9, 53.8, and 72.9 mm long) from 3.2 mm diameter nests, 2 female cells (40.2 and 107.4 mm long) and 1 male cell (97.1 mm long) from 4.8 × 155 mm nests.

<sup>b</sup> Female cell length in 4.8 × 155 mm nests was significantly greater than in 4.8 × 75 mm nests ( $t = 2.95$ ,  $df = 98$ ,  $P < 0.05$ ).

<sup>c</sup> Male cell length in 3.2 × 85 mm nests was significantly greater than in 4.8 × 155 mm nests ( $t = 4.07$ ,  $df = 134$ ,  $P < 0.05$ ), and in 4.8 × 155 mm nests male cell length was significantly greater than in 4.8 × 75 mm nests ( $t = 1.75$ ,  $df = 46$ ,  $P < 0.05$ ).

<sup>d</sup> Female cells were significantly longer than male cells in 4.8 × 75 mm nests ( $t = 2.04$ ,  $df = 80$ ,  $P < 0.05$ ).

females for every male (45 ♂♂:91 ♀♀), whereas 3.2 mm diameter nests produced more than 8 males for every female (166 ♂♂:20 ♀♀). The difference in sex ratios between 3.2 and 4.8 mm diameter nests was significant ( $\chi^2 = 109.69$ ,  $df = 1$ ,  $P < 0.05$ ).

The arrangement of male and female cells within the nests was nonrandom. Table 5 shows that cells at the inner end of the nests produced mostly males with a progressively greater proportion of females reared from cells closer to the entrance. The trend was most apparent in the 3.2 mm diameter nests. In all 3 trap-nest sizes, the observed frequencies of males and females in each cell position were significantly different from frequencies expected if the probability of a male or female being produced was the same for each cell position (3.2 × 85 mm trap-nests— $\chi^2 = 28.48$ ,  $df = 4$ ,  $P < 0.01$ ; 4.8 × 75 mm trap-nests— $\chi^2 = 9.48$ ,  $df = 4$ ,  $P < 0.01$ ; 4.8 × 155 mm trap-nests— $\chi^2 = 10.33$ ,  $df = 4$ ,  $P < 0.01$ ). However, there was no significant difference between the first 6 cell positions in 4.8 × 75

Table 4. Head widths and cocoon dimensions of *Trypoxylon vagulum* reared from trap-nests. Measurements are in mm.

	Trap-nest tube diameter			
	3.2		4.8	
	Males	Females	Males	Females
Head width <sup>a</sup>				
Range	1.9–2.3	2.0–2.3	2.0–2.3	2.1–2.4
Mean ( <i>n</i> )	2.1 (86)	2.2 (18)	2.2 (31)	2.3 (56)
Cocoons				
Length				
Range	7.7–9.8	8.8–10.8	8.1–10.1	8.1–10.3
Mean ( <i>n</i> )	8.8 (82) <sup>b</sup>	9.7 (16) <sup>b</sup>	8.9 (27) <sup>c</sup>	9.5 (49) <sup>c</sup>
Width at center				
Range	2.3–2.9	2.4–3.1	2.7–3.6	3.0–3.8
Mean ( <i>n</i> )	2.6 (82) <sup>b</sup>	2.7 (16) <sup>b</sup>	3.1 (27) <sup>c</sup>	3.4 (49) <sup>c</sup>
Greatest width (near anterior)				
Range	2.3–3.1	2.4–3.2	3.0–4.1	3.2–4.4
Mean ( <i>n</i> )	2.7 (82)	2.9 (16)	3.5 (27)	4.0 (49)
Correlation of head width and cocoon length				
<i>r</i> ( <i>n</i> )	0.75 (56)	0.84 (16)	0.36 (21)	0.67 (45)

<sup>a</sup> Mean head widths of both sexes reared from 3.2 mm diameter nests were significantly smaller than those of the same sex reared from 4.8 mm nests (males— $t = -3.56$ ,  $df = 115$ ,  $P < 0.05$ ; females— $t = -3.51$ ,  $df = 72$ ,  $P < 0.05$ ).

<sup>b</sup> In 3.2 mm diameter nests female cocoons were significantly longer ( $t = 6.88$ ,  $df = 96$ ,  $P < 0.05$ ) and wider at the center ( $t = 4.89$ ,  $df = 96$ ,  $P < 0.05$ ).

<sup>c</sup> In 4.8 mm diameter nests female cocoons were significantly longer ( $t = 6.53$ ,  $df = 74$ ,  $P < 0.05$ ) and wider at the center ( $t = 6.92$ ,  $df = 74$ ,  $P < 0.05$ ) than male cocoons.

mm and 4.8 × 155 mm trap-nests. Therefore, for a given cell position the probability of a male or female being produced is the same in the 4.8 × 75 mm and 4.8 × 155 mm diameter nests. There were significant differences in the frequencies of males and females produced at each cell position in 4.8 mm and 3.2 mm diameter trap-nests (cell position 1,  $\chi^2 = 28.49$ ; pos. 2,  $\chi^2 = 28.88$ ; pos. 3,  $\chi^2 = 29.83$ ; pos. 4,  $\chi^2 = 14.53$ ; pos. 5–6,  $\chi^2 = 9.00$ ,  $df = 1$ , and  $P < 0.01$  for all tests).

*Growth and development of the immature stages.*—Female wasps always glued the egg onto the abdomen of one of the largest spiders in the nest, but the egg's position varied. The egg is pearly white, sausage-shaped, 1.8 mm long ( $n = 3$ ), and 0.5–0.8 mg in weight ( $n = 2$ ). Under the unnaturally fluctuating but generally cool conditions in the air conditioned laboratory, elapsed time from oviposition to emergence of the adult was 26–64 days. Development may take only 21–28 days under natural conditions. In a typical sequence, the embryo required less than 2 days to develop. The first instar larva punctured the surface of the egg and the cuticle of the attached spider's abdomen. For the first 2 days, it fed upon that spider, completely consuming it. By that time, its growth had become so rapid that in only another 2–4 days it had devoured all of the remaining spiders. Within another 3 days, it had completed its cocoon and entered the prepupal stage.

Table 5. Distribution of male and female cells in nests of *Trypoxylon vagulum* from trap-nests.<sup>a</sup>

Trap-nest size in mm	No. of nests		Cell position numbered from inner end of the nest toward the entrance					
			1	2	3	4	5-6	7-9
3.2 × 85 <sup>b</sup>	54	No. males	42	36	31	22	12	—
		No. females	0	2	3	6	9	—
4.8 × 75 <sup>b</sup>	30	No. males	12	4	5	5	2	—
		No. females	10	8	11	8	18	—
4.8 × 155 <sup>b</sup>	35	No. males	13	6	4	7	4	3
		No. females	10	12	14	12	15	15

<sup>a</sup> Nests used to compile this table all began at the inner end of the trap-nest tube.

<sup>b</sup> Observed frequencies of males and females at each cell position were significantly different at  $P < 0.01$  from expected frequencies for all trap-nest sizes (3.2 × 85 mm traps— $\chi^2 = 28.5$ ,  $df = 4$ ; 4.8 × 75 mm— $\chi^2 = 9.48$ ,  $df = 4$ ; 4.8 × 155mm— $\chi^2 = 10.33$ ,  $df = 5$ ).

The prepupal stage lasted for 6 or more days and the pupal stage for another 16 or more days. After the wasp moulted to the adult stage, it remained quiescent for several days, before attempting to cut its way out of its cocoon and leave the nest.

The fragile cocoons (Figs. 1 and 2) were thin and brittle. They had a varnished, reddish-brown appearance with a gray anterior end. Their shape was influenced by the diameter of the nest. In 4.8 and 6.4 mm diameter nests, the cocoons were robust (Fig. 2) with bulbous anterior ends. In 3.2 mm diameter nests, the cocoons were slender (Fig. 1) with the anterior ends flaring outward to the walls of



Figure 1. Cocoons of *Trypoxylon vagulum* taken from a 3.2 mm diameter trap-nest. The scale at the bottom is in mm.





Figure 2. Cocoons of *Trypoxylon vagulum* taken from a 4.8 mm diameter trap-nest. The scale at the bottom is in mm.

the trap-nest tubes. Female cocoons averaged longer and wider at the center than male cocoons (Table 4), but were otherwise indistinguishable from those of males.

*Parental Investment in male and female progeny.*—Larval cells were provisioned with 7 to 35 ( $n = 51$ ) spider prey and the wet weight biomass of all spiders in a cell ranged from 33.4 to 65.4 mg ( $n = 41$ ). We reared 16 females and 11 males of *T. vagulum* from cells in which the number of prey and total wet weight biomass of the prey were determined (Table 7). The difference in number of spiders between male and female cells was not significant but female cells did have a significantly greater total wet weight biomass of prey than male cells ( $t = 6.65$ ,  $df = 25$ ,  $P < .05$ ).

Besides the difference in biomass of provisions for male and female cells, there is probably a difference in the biomass of provisions in cells from 3.2 mm and 4.8 mm diameter nests. The evidence is based upon head widths (HW) of adult wasps produced from cells in these two sizes of nests (Table 4). Males reared from 3.2 mm diameter nests were significantly smaller than males from 4.8 mm diameter nests (Table 4). Likewise, females produced from 3.2 mm diameter nests were significantly smaller than females produced from 4.8 mm diameter nests (Table 4). Because the developing larvae normally consume all the provisions in their cells, the difference in size of adults produced from 3.2 and 4.8 mm diameter nests is probably related to the amount of provisions available to them as larvae.

*Prey preferences.*—*Trypoxylon vagulum* preyed upon several families of spiders (Table 9). Most prey were snarebuilding spiders, among which Araneidae predominated, but occasional Tetragnathidae, Theridiidae and Uloboridae were also found. Wandering spiders consisted of a juvenile Ctenidae, juvenile Clu-

Table 6. Mortality in brood cells of *Trypoxylon vagulum* obtained from trap-nests.<sup>a</sup>

	Trap-nest tube size in mm			
	3.2 × 85	4.8 × 155	4.8 × 75	6.4 × 155
No. of nests	68	33	13	2
No. of cells	245	167	54	8
No. of males reared	166	37	8	—
No. of females reared	20	71	20	3
Losses due to unknown factors				
Moldy cells	7	1	—	—
Dead egg or egg not found	5	11	2	—
Dead larva	2	—	—	—
Dead prepupa or pupa	16	8	2	—
Losses due to enemies				
Bombyliidae (Diptera)				
<i>Lepidophora trypoxylona</i>				
Hall	4	4	2	—
<i>Anthrax</i> sp.	—	1	—	—
Sarcophagidae (Diptera)				
<i>Amobia erythrura</i> (Wulp)	—	10	16	—
Phoridae (Diptera)				
<i>Phalacrotophora punctiapex</i>				
Borgmeier	13	19	4	5
Rhipiphoridae (Coleoptera)				
<i>Macrosiagon lineare</i>				
(Le Conte)	2	—	—	—
Chrysididae (Hymenoptera)				
<i>Trichrysis nigropolita</i>				
(Bischoff)	7	2	—	—
Ichneumonidae (Hymenoptera)				
<i>Polyphaga</i> sp. (?)				
	—	1	—	—
Formicidae (Hymenoptera) <sup>b</sup>				
	2	3	—	—
Total Losses	59	55	26	5

<sup>a</sup> Nests used to compile this table were ones in which all wasp larvae and parasites had completed their larval stages before the nests were opened.

<sup>b</sup> Ants were such a problem that during most of the study we tried to exclude them by coating the trap-nest wires with Tanglefoot®. Hence, the mortality due to ants is not representative.

bioniidae, and 2 juvenile Pisauridae. Although *T. vagulum* primarily takes snare-building spiders, we could not determine if the prey were taken from webs or other situations, because the diurnal behavior of the prey is variable (Griswold & Coville 1986). For example, the prey could have been hiding near a web or hiding without a web. Only for *Cyclosa* and *Micrathena* can we be sure that they were taken from webs, as we always observed these genera in webs during the day.

Mostly small immature spiders comprised the prey of *T. vagulum*. The distribution of size classes of the prey by number and biomass is skewed toward the small sized prey (Fig 3). Although individual weights of spider prey ranged from 0.2 to 21.3 mg, 64% of the prey weighed 2.0 mg or less.

Table 7. Amount of provisions in male and female cells of *Trypoxylon vagulum*.

	Male Cells ( <i>n</i> = 11)	Female Cells ( <i>n</i> = 16)
No. of spiders		
range	10–28	11–35
mean ± SD	18.3 ± 5.3	19.6 ± 5.9
Total wet weight biomass of provisions <sup>a</sup>		
range	33.4–47.9	41.7–65.4
mean ± SD	41.5 ± 5.0 <sup>a</sup>	51.6 ± 5.68 <sup>a</sup>

<sup>a</sup> Wet weight biomass of provisions was significantly greater in female cells than male cells ( $t = 6.65$ ,  $df = 25$ ,  $P < 0.05$ ).

*Mortality and Natural Enemies.*—We have no information on mortality of adult wasps, but Table 6 summarizes the mortality occurring in brood cells. All of the nests used to compile the table were collected from the field within a few days of their completion. A greater mortality probably would have been evident if the nests had been left in place, because many would probably have been discovered by enemies capable of digging their way through the closure plugs or ovipositing through walls of the trap-nests.

The greatest losses (48% of the cells) occurred in short ( $4.8 \times 7.5$  mm) trap-nests, but this is more related to their being only set out at the living quarters where natural enemies were especially abundant. The  $3.2 \times 85$  mm traps and  $4.8 \times 155$  mm traps were distributed in equal numbers among all habitats. The brood cells from  $3.2 \times 85$  mm traps suffered significantly less mortality (24% of the

Table 8. Mortality of immature stages of *Trypoxylon vagulum* in the first 2 and last 2 cells in completed nests.<sup>a</sup>

	First 2 cells of nest	Last 2 cells of nest
$3.2 \times 85$ mm nests ( <i>n</i> = 38) <sup>b</sup>		
No. of cells	76	76
No. of adults reared	63	61
Losses <sup>c</sup>	13	15
$4.8 \times 155$ mm nests ( <i>n</i> = 2) <sup>b</sup>		
No. of cells	44	44
No. of adults reared	28	29
Losses <sup>c</sup>	16	15
$4.8 \times 75$ mm nests ( <i>n</i> = 9) <sup>b</sup>		
No. of cells	18	18
No. of adults reared	7	6
Losses <sup>c</sup>	11	12

<sup>a</sup> Nests used in this study were selected by the following criteria: 1) All wasp larvae and parasites had completed their larval stages before the nests were opened, and 2) the nests contained 4 or more cells.

<sup>b</sup> Number of nests.

<sup>c</sup> Losses in the first 2 and last 2 cells were not significantly different.

Table 9. Prey preferences of *Trypoxylon vagulum*.

Spider Prey	Number of Prey
<b>Araneidae</b>	
<i>Eustala</i> sp. #1	54
<i>Eustala</i> sp. #2	4
<i>Eustala</i> sp. #3	6
<i>Eustala</i> miscellaneous juveniles	93
<i>Verrucosa</i> sp.	89
<i>Acacesia</i> sp.	74
<i>Wagneriana tauricornis</i>	2
<i>Wagneriana</i> sp. #1	21
<i>Wagneriana</i> sp. #2	4
<i>Wixia</i> or <i>Parawixia</i> sp.	9
<i>Micrathena</i> sp.	47
<i>Gasteracantha</i> sp.	5
<i>Scoloderus</i> sp.	1
<i>Cyclosa</i>	2
undetermined sp. #1	6
undetermined sp. #2	5
undetermined sp. #3	78
<b>Clubionidae</b>	
<i>Clubionia</i> sp.	1
<b>Ctenidae</b>	
undetermined sp. #1	1
<b>Pisauridae</b>	
undetermined sp.	2
<b>Tetragnathidae</b>	
undetermined sp. #1	1
undetermined sp. #2	1
undetermined sp. #3	1
undetermined sp. #4 ( <i>Tetragnatha</i> )	1
undetermined sp. #5	1
<b>Theridiidae</b>	
undetermined sp. #1	1
<b>Uloboridae</b>	
<i>Miagrammopes</i>	9
undetermined sp. #1	5
undetermined sp. #2	1

cells) than did the brood cells from  $4.8 \times 155$  mm traps (33% of the cells) ( $X^2 = 3.89$ ,  $df = 1$ ,  $P < 0.05$ ).

We suspected that the longer a nest was being constructed the greater the probability of its discovery by natural enemies. If this is the case, we could expect a greater mortality in the last cells to be provisioned than in the first cells provisioned. Nevertheless, our data did not support this contention. In completed nests with a total of 4 or more cells, losses in the first 2 and last 2 cells were not significantly different (Table 8).

The natural enemies listed in Table 6, exhibit diverse modes of attacking nests of *T. vagulum*. Adults of the bombyliid flies *Lepidophora trypoxylona* Hall and

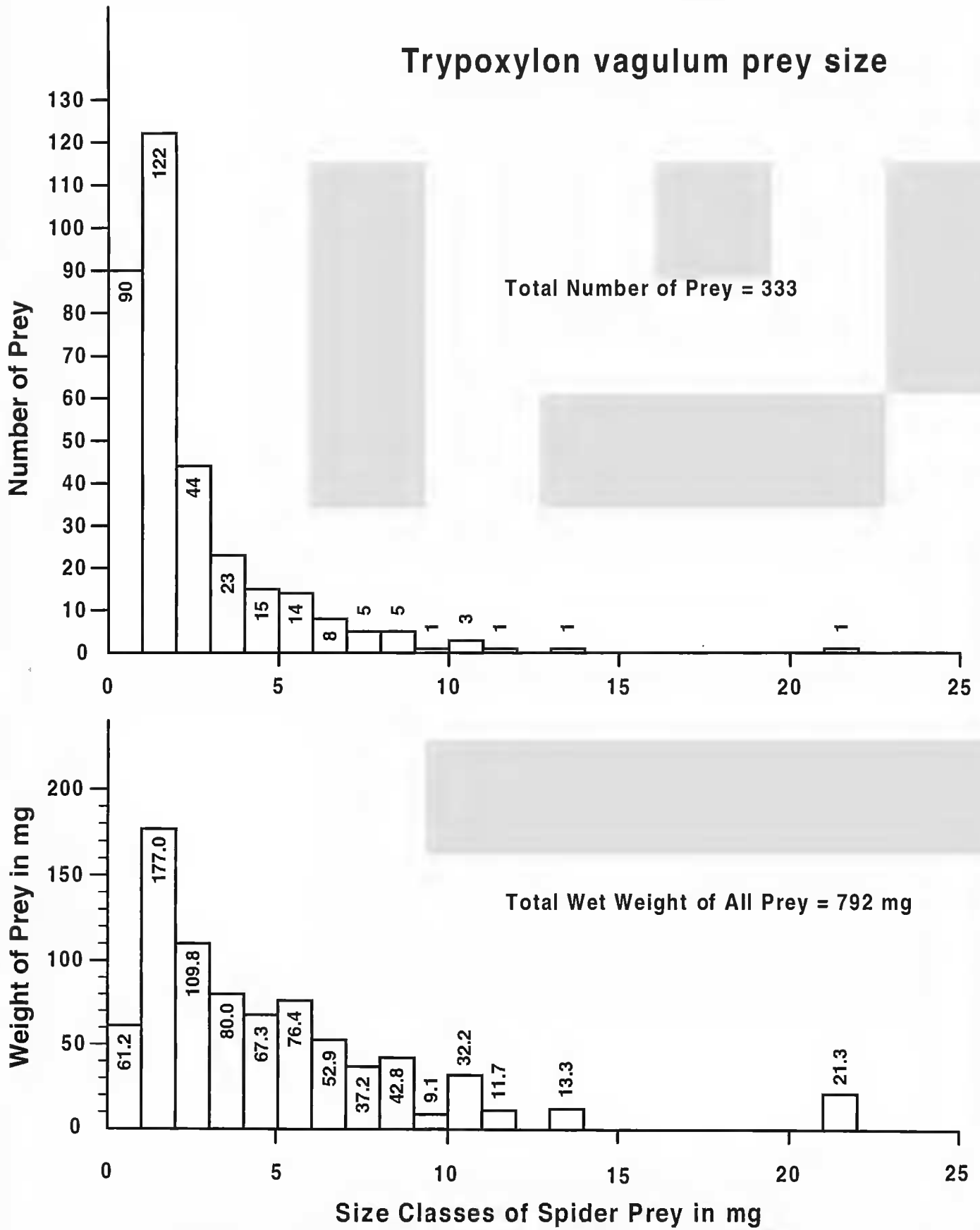


Figure 3. Size classes of prey taken from nests of *Trypoxylon vagulum*. The top bar graph breaks down the size classes by the number of spiders occurring in each class. The bottom bar graph breaks down the size classes by the total wet weight of all spiders in each class.

*Anthrax* sp. hovered in front of nests while presumably ejecting microscopic first instar larvae at the entrance opening. The larva of *Anthrax* developed as a parasitoid upon a single wasp larva. Before attacking its host the *Anthrax* larva presumably waited until the host larva had completed its feeding, because the *Anthrax* adult emerged from a completed cocoon of *T. vagulum*. *Lepidophora trypoxylona* was more destructive. Its larva first killed the host egg or young larva and then consumed the spider prey by sucking the contents out of their bodies.

Larvae of *L. trypoxylona* commonly invaded additional cells if there were insufficient food in the initially infested cell. Pupae of both bombyliids possessed powerful cephalic teeth that enabled them to dig their way out of nests shortly before emergence of the adult fly.

The sarcophagid fly, *Amobia erythrura* (Wulp) was only found at the living quarters, but was very destructive in 4.8 mm diameter nests of *T. vagulum* at that site. None of the 3.2 mm diameter nests were attacked. Adults of *A. erythrura* stationed themselves near bundles of trap-nests and attempted to follow prey laden females of *T. vagulum* into their nests. Successful attacks resulted in a cell being infested by 1 to 7 maggots. The maggots appeared to work in unison, first attacking the wasp egg, and then consuming the spider prey. *Amobia* maggots always worked their way toward the nest entrance and destroyed every cell in their path. Once at the nest entrance they bored their way partially through the closure plug and then pupated. The adult *Amobia* usually could punch their way through the remaining part of the closure plug and escape the nest. In one nest the maggot failed to work its way to the entrance and the adult fly being unable to punch its way out of the nest died next to its puparium.

The phorid fly, *Phalacrotophora punctiapex* Borgmeier is a small (3–4 mm long), fast running insect that frequented the entrances of wasp nests. Adults of *P. punctiapex* entered nests by evading the host wasps. Once in the nest the flies hid among the spider prey and proceeded to lay many eggs on the walls and mud partition at the inner end of the cell. The newly emerged maggots first attacked and consumed the host wasp egg and then fed upon the spider prey. Often the maggots invaded additional cells by burrowing through the cell partitions. Nevertheless, the maggots seldom made their way to the nest entrance. Instead, they pupated within a brood cell. Their puparia were strongly glued to the walls of the trap-nest tube. It is unclear to us as to how *P. punctiapex* escape the nests. The adults have no obvious digging structures for penetrating cell partitions, and they generally seem to emerge before the host wasps. Cells of *T. vagulum* were infested by 1–15 maggots and one nest contained 34 maggots.

An adult of the rhipiphorid beetle, *Macrosiagon lineare* (Le Conte) was reared from each of 2 cocoons of *T. vagulum*. The cocoons were from different nests.

The chrysidid wasp, *Trichrysis nigropolita* (Bishoff), was reared from cells of *T. vagulum*, although we did not observe any successful attacks. Adult chrysidids waited at the nest entrances for an opportunity to enter an unguarded nest and oviposit into a newly provisioned cell. Coville & Coville (1980) observed this chrysidid species chewing holes through outer cell partitions and suspected that they can oviposit into a cell through such a hole.

An occasional spider that was brought into the nest was parasitized by an ichneumonid (*Polyphaga* sp.). In one cell the ichneumonid completed its development and spun a cocoon. On emerging the ichneumonid in attempting to escape from the nest killed a *T. vagulum* pupa.

Probably the most severe enemies of wasps at La Selva were the numerous species of ants. At the living quarters *Monomorium floracula* (Jerdon) and *Tetramorium bicarinatum* (Nylander) were the principal nest raiders. At other sites several other ant species nested in trap-nests or raided them. These included *Camponotus abdominalis* Mayr, *Camponotus planatus* Roger, *Crematogaster limata palans* Forel, *Pachycondyla unidentata* Mayr, *Paratrechina caeciliae* Forel, *So-*

*lenopsis picea* Fomery, and *Solenopsis* sp. Many of these species and especially *Tetramorium* and *Monomorium* were capable of digging through closure plugs and looting completed nests. Male wasps were usually able to thwart individual foraging ants but if ants were able to gain entrance to the nest through temporary absence of the male or by overwhelming him, the nest was lost. As noted in Table 6, we coated the wires supporting trap-nest bundles with Tanglefoot® to discourage ants from attacking nests. Otherwise, ants would have destroyed many more nests.

Brockmann (1992) reported chalcid wasps in the genus *Mellitobia* attacking nests of *T. monteverdeae* Coville from Monteverde, Costa Rica. Nevertheless, we encountered no chalcids in nests *T. vagulum* or any other *Trypoxylon* species from La Selva.

*Nest supercedure.*—Four traps from which *T. vagulum* were reared also contained cells of other species of wasps and bees. In the arboretum a 4.8 × 155 mm trap had one cell of *T. vagulum* at the inner end of the tube. On top of the cell were two empty cells and then a 4-celled nest of an undetermined species of *Trypoxylon*. At the living quarters a 4.8 × 155 mm nest had 1 cell of *T. (Trypargilum) majus* Richards followed by a 3-celled nest of *T. vagulum*. Another 4.8 × 155 mm nest at the living quarters had 1 cell of *T. vagulum* 49.4 mm from the inner end of the tube followed by 2 cells of a resin bee (Megachilidae). Also at the living quarters a 3.2 × 85 mm trap had two cells of *T. vagulum* at the inner end of the tube followed by a 2-celled nest of an eumenid wasp.

*Behavioral observations.*—Our observations took place at the living quarters. *Trypoxylon vagulum* was one of several species in the subgenus *Trypargilum* that nested in trap-nests at the living quarters. *Trypoxylon lactitarse* Saussure and an undetermined sibling species (C, corresponds to Sp. C in Griswold & Coville 1986) were almost as abundant as *T. vagulum*. Another undetermined species (A, corresponds to Sp. A in Griswold & Coville 1986), related to *T. nitidum* Smith, was also abundant. *Trypoxylon saussurei* Rohwer and *T. majus* were occasional trap-nest occupants in 1980.

*Trypoxylon vagulum* was the only species to use 3.2 mm diameter trap-nests, but it did compete with *T. saussurei*, *T. majus*, and species A for 4.8 mm diameter nests. There was little direct competition, however, because we insured that several empty trap-nests were continuously available to the wasps. *Trypoxylon lactitarse* and species C only used trap-nests with diameters of 6.4 mm or larger.

During fair weather, *T. vagulum* were active from 1 to 2 hours after sunrise until 1.5 to 2.5 hours before sunset. They ceased their foraging and nest construction activities during rainy spells.

Like most *Trypoxylon* wasps in the subgenus *Trypargilum*, a male of *T. vagulum* would pair with a female that was initiating a nest. Thereafter he would guard the nest while the female hunted for spiders or foraged for mud. During the day the male usually remained face outward at the nest entrance and would snap his mandibles at potential intruders, such as ants. The male seldom left the nest unguarded for more than a few minutes. Occasionally they did leave for 5–15 minutes, when the female was present. The male would often leave his nest to pursue or rarely butt unpaired males of *T. vagulum* that alighted on or hovered near his nest. Nevertheless, we never observed males of *T. vagulum* grappling with one another or physically trying to usurp another male's nest. In contrast,

males of *T. lactitarse* and species C often engaged in fights and attempted to invade one another's nest.

Active nests of *T. vagulum* always had a male associated with them. In fact, a female of *T. vagulum* would not leave to forage unless a male was in the nest. At night the female would remain in her nest, whereas a male would be present or absent.

One or two males would follow females that were searching for new nest sites. So pair formation usually took place even before a new nest had been initiated.

When searching for a new nest, a female of *T. vagulum* in a slow hovering flight would move along the surface of objects such as beams, railings, posts, etc. She would frequently alight to examine dark spots and small holes, which she would attempt to enter headfirst. If the tubular cavity within a hole was potentially suitable for a new nest, she would begin to clean it out. Otherwise, she would resume her search.

In preparing a new nest site the female would remove any material blocking or constricting the tube. The material included loose debris as well as mud and frass that adhered to the walls of the tube. She would use her mandibles to scrape the surface of the tube. With a load of debris cradled with her mandibles and front legs she would back out of the nest and either immediately drop the load or take flight and drop the load 3–50 cm from the nest entrance. Once the nest had been cleaned, she would then leave the nest and return with a load of mud. She used the mud for the preliminary plug at the inner end of the nest. Several loads of mud were required for the plug.

Females of *T. vagulum* were observed obtaining mud from nests of mud-daubing wasps, especially those of *Trypoxylon* (*Trypargilum*) species in the Abitarse Group (see Coville 1982, for classification) and *T. (Trypoxylon) fabricator*. Females apparently carried water that they regurgitated to soften the hard mud on nests of the host wasps. They then removed a small ball of mud with their mandibles and transported it to their own nest. We were unable to determine if *T. vagulum* uses other sources of mud. We did not observe them at muddy spots frequented by other species of *Trypoxylon*.

Once the preliminary plug was completed, the female began to forage for spiders. Females usually returned to their nests with spiders within 6–15 minutes, but foraging flights as short as 2 minutes and longer than 1 hour were also observed. On returning to the nest with a spider the female would alight at the entrance. The male, after tapping the female's antennae with his own, would leave the nest and climb upon the female's back. The female would then enter the nest with the male following her. Once inside the nest the male would often invert himself, climb beneath the female and grip the base of her petiole with his mandibles. In this manner the pair would proceed further into the tube, until the female dropped her spider.

During the early stages of provisioning, the female often merely deposited the spider, groomed herself and then left on the next foraging trip. After the female's departure the male would pack the spiders tightly into the mass of provisions by butting the spider with his head. When the cell was almost fully provisioned, the female would usually pack the spiders with her head as well.

Within nests in 3.2 mm diameter grooves in observation trap-nests there was insufficient space for the wasps to turn around. They would first have to leave



the nest in order to reverse their position. Within 4.8 mm diameter grooves the wasps were able to turn around.

After the final spider had been obtained the female would usually leave the nest for a few minutes. On returning she would inspect the prey, firmly pack them with her head, and then groom herself. When she was ready to oviposit, she would back out of the nest, reverse her position, back into the nest, and begin probing the mass of spiders for a suitable abdominal surface upon which to oviposit. During oviposition, she remained motionless.

We observed 10 cells of *T. vagulum* continuously from initiation through oviposition. In addition, we made numerous more fragmentary observations on provisioning and oviposition in other cells. Nevertheless, mating was never observed, although a male was present at all times. This was in direct contrast to *T. lactitarse* and species C in which mating took place immediately before oviposition in almost every case. In fact, unless mating had occurred, males of the latter two species would disrupt their mate's attempt to oviposit.

Of the 10 ovipositions observed in *T. vagulum*, 7 males were reared from the resulting eggs (the other 3 rearing attempts failed). In *T. lactitarse* and species C, eggs resulting from ovipositions preceded by mating produced males and females; in the 1 case in which mating did not precede oviposition, the egg failed to develop.

After oviposition, the female would begin construction of the cell partition to seal the cell. She spread her first load of mud in a thin band across the bottom of the tube in front of the provisions. She spread the mud with her mandibles and simultaneously vibrated her flight muscles, which emitted a buzzing sound audible for about 1 meter from the nest. Several loads of mud were required to complete a partition. During the final stages her body would rotate so that she could spread mud across the roof of the tube and complete the closure of the cell. The male watched the female or held onto her petiole with their mandibles while she spread the mud. We did not observe males assisting females in construction of partitions or closure plugs.

#### DISCUSSION

We chose to follow the classification provided by Coville (1982), in which the genus *Trypoxylon* is divided into the subgenera *Trypoxylon* and *Trypargilum*. The two subgenera are distinguished on the basis of a several of morphological characters. *Trypargilum*, confined to the Western Hemisphere, also differs in the widespread occurrence of male guarding of nests and the generally darker and harder cocoons. Unless specifically stated, the following discussion is restricted to species of the *Trypoxylon* species in the subgenus *Trypargilum*.

Most authors have informally recognized several species groups and complexes of *Trypargilum* (Richards 1934, Krombein 1967a, Krombein 1979, Coville 1982). Three groups are fairly well defined morphologically; the Albitarse Group, the Superbum Group, and the Nitidum Group (Bohart & Menke 1976, Coville 1982). The Albitarse Group contains all species that build mud nests, generally in the form of a series of vertical mud tubes. The other groups nest in pre-existing tubular cavities. The Superbum Group, recognized by a transverse carina on the frons, only contains a few tropical species. The Nitidum Group encompasses the majority of species. It is a heterogeneous collection divided, not always success-

fully, into several species complexes. *Trypoxylon vagulum* is a member of the vagum complex (see Coville 1982). Krombein (1967b) and Matthews & Matthews (1968) found that nest architecture, cocoon structure and prey preferences seem to vary according to the species groups and complexes. Subsequent studies have continued to build upon that framework.

Overall, the nest structure of *T. vagulum* resembles that of other species of the Nitidum and Superbum groups, although because of its small size it is able to use smaller diameter nests than any species studied so far. As with most species, *T. vagulum* built the closure plugs at the nest entrance. Two species diverge from this pattern by having the closure plugs recessed from the entrance. One of these species is *T. superbum* (Coville & Griswold 1984) of the Superbum Group. The other is *T. xanthandrum* (Coville & Griswold 1983) of the Nitidum Group's fugax complex. Among all species of *Trypargilum* observed at La Selva, the outer surface of plugs of *T. vagulum* were distinctive in that they were smoothly concave and their mud was never spread onto the outer surface of the trap-nest itself. Other species were not so neat.

*Trypoxylon vagulum* seems to obtain mud for its nests from the mud nests of other *Trypoxylon* wasps, particularly *T. (Trypoxylon) fabricator*. At typical sites where many species of *Trypoxylon* of both subgenera mine mud, such as muddy spots along trails, *T. vagulum* was absent in our observations, despite being the most abundant species trap-nested. Nevertheless, we do not feel that we can totally discount the possibility that *T. vagulum* may occasionally use such sites.

Genaro (1996) found that the inner walls of cell partitions of *T. (Trypargilum) subimpressum* Smith (excavatum complex) generally have a glob of mud appressed to them which is mined by the larva for incorporation into its cocoon. In freshly provisioned cells of *T. vagulum*, the inner walls of cell partitions were generally smoothly concave, and we noticed no mud globs adhering to them. Nevertheless, the larvae did mine the inner partitions for mud during cocoon spinning, as reported by Genaro (1996). This is probably typical of the wasps in the subgenus. In our own observations of larvae spinning cocoons, the larvae sometimes appear to be regurgitating material into the cocoon matrix.

Cocoons of *T. vagulum* are distinct from all other species in the subgenus *Trypargilum*, not only by their small size, reflecting the small size of *T. vagulum* compared to other *Trypargilum* (Coville 1982), but also by their shape. In this species, as the nest diameter becomes larger, the cocoons become more globular with the anterior end distinctly swollen (Fig. 2) but not flaring outward. This outward flare is frequently seen in species of the punctulatum complex (see Krombein 1967b, Camillo et al. 1993, 1994; Coville 1981, 1982), fugax complex (Coville & Coville 1980, Coville & Griswold 1983), and Superbum group (Coville & Griswold 1984). In these and other species, the cocoon diameter at the middle does not increase greatly with nest diameter increase, as it does in *T. vagulum*. Compared with other species of *Trypargilum* we observed at La Selva including *T. lactitarse*, *T. superbum*, *T. xanthandrum*, *T. vagum* Richards, *T. agamemnon* Richards, *T. saussurei*, *T. majus*, and a couple of undetermined species the cocoons of *T. vagulum* appeared to be somewhat lighter in color and more fragile.

Among *Trypargilum* species that normally nest in pre-existing cavities (Superbum and Nitidum Groups), nests generally have a non-random distribution of male and female cells. There are two trends. First, for a given species, the smallest

acceptable diameter nests produce mostly males. The proportion of females increases in larger diameter nests. When cells of both sexes are present, male cells, with few exceptions, occur more frequently at the inner end of the nests. In some species, such as *T. tenoetilan* Richards (Coville & Coville 1980), *T. tridentatum* Packard (Krombein 1967b, personal observation) and *T. lactitarse* (Krombein 1967b, under the name *striatum*) in North America, male and female cells are clearly segregated with male cells at the inner end and female cells toward the entrance. In other species, such as *T. vagulum*, *T. clavatum* Say (Krombein 1967b), *T. collinum collinum* Smith (Krombein 1967b), *T. lactitarse* (Camillo et al. 1993) in Brazil, and *T. rogenhoferi* Kohl (Camillo et al. 1994), male and female cells are frequently intermixed. Nevertheless, the probability of a given cell being a male or female cell still relates to its position in the nest. One exception, may be *T. collinum rubrocinctum* (Packard) in which Krombein (1967b) reported female cells to be at the inner end and males at the outer end. In contrast, species that build mud nests (Albitarse Group), such as *T. politum* Say (Brockmann & Grafen 1989) and *T. monteverdeae* (Brockmann 1992), appear to have a random distribution of male and female cells in the mud tubes.

In the present study, we also found that males and females reared from small 3.2 mm diameter nests were significantly smaller than individuals of the same sex from 4.8 mm diameter nests. Among wasps reared from the same diameter nests, we found no correlation between size of the wasps and cell length.

Prey preferences of *Trypargilum* vary widely (Matthews & Matthews 1968, Coville 1982, Griswold & Coville, 1986). Among species of the Albitarse Group studied, prey consist entirely of orbweaving spiders of the family Araneidae, principally among the genera *Eustala*, *Neoscona*, and, less frequently, *Araneus* (see review of Coville 1982, Brockmann & Grafen 1992 on *T. politum*, Brockmann 1992 on *T. monteverdeae*). The only species of the Superbum Group so far studied, *T. superbum* (Coville & Griswold 1984, Griswold & Coville 1986), specializes on Salticidae. Among species in the Nitidum Group, prey preferences vary from extremely narrow to broad. For example, *T. xanthandrum* of the fugax complex appears to specialize on spiders of the family Senoculidae, a poorly known group of wandering spiders (Coville & Griswold 1983, Griswold & Coville 1986). *Trypoxylon tenoetilan* of the fugax complex (Coville & Coville 1980), and species in the spinosum complex normally take a wide variety snarebuilding and wandering spiders (see review of Coville 1982) found on vegetation and manmade structures. Data of Genaro et al. (1989) indicate that *Trypoxylon subimpressum* of the excavatum complex may also fall into this later category.

*Trypoxylon vagulum* preys almost entirely on snarebuilding spiders. This strong preference for snarebuilding spiders is shared with species of the nitidum complex, *T. orizabense* Richards, and *T. tridentatum* (see review of Coville 1982, O'Brian 1982, Coville 1986, Jiménez & Tejas 1994). Species in the punctulatum complex also show a preference for snare building spiders (see review of Coville 1982, Camillo et al. 1993 on *T. lactitarse*, 1994 on *T. rogenhoferi*). A preference for snare-building spiders does not necessarily mean that the wasps hunt for spiders that are in webs. Griswold & Coville (1986, Table 2) noted that the diurnal habits of prey of *T. vagulum* at La Selva fall into 5 patterns, all but the last pertain to snarebuilding species: 1) on intact web (eg., *Cyclosa*, *Micrathena*, and *Verrucosa*); 2) at the edge of intact webs (eg., araneid undetermined sp. #3); 3)

cryptic on substrate, no retreat, intact web present (eg., *Eustala*); 4) cryptic on substrate, retreat and web absent (eg., *Acacesia*); 5) motionless, exposed on foliage (Clubionidae and Ctenidae).

Brockmann & Grafen (1989) showed that females of *T. politum* provision male cells with less biomass of spiders than female cells. This is also the case with *T. vagulum*, even though we found no significant difference in the number of prey in male and female cells.

Camillo et al. (1993) found that brood cells nearest the entrance in nests of *T. lactitarse* suffered the greatest mortality. This seems logical for a couple of reasons. First, some enemies such as the bombyliid fly *Lepidophora*, phorid fly *Phalacrotophora*, and sarcophagid flies may destroy many or all of the cells between the initially infested one and the nest entrance. Second, some enemies attack completed nests. Among these, some can oviposit through the closure plug while others such as certain mutillid wasps, and some ants, burrow through the closure plug. Although we found no significant difference in the mortality rates between the first two and last two cells in *T. vagulum* nests (Table 8), our data are irrelevant with regard to ants and enemies that attack completed nests. We used Tanglefoot® to discourage attacks by ants before and after nest completion. In addition, we collected nests from the field within a few of days of completion. This artificially reduced their vulnerability to enemies that attack completed nests.

Studies by Brockmann & Grafen (1989) on *T. politum*, Brockmann (1992) on *T. montevedae*, Coville & Coville (1980) on *T. tenocitlan*, and our own unpublished observations on *T. lactitarse* and species C indicate that mating takes place in the nest. In particular, mating seems to take place just before oviposition, when the male becomes particularly sexually aggressive. Nevertheless, with *T. vagulum* we observed no matings inside or outside of nests. Do they mate away from the nests or before nesting begins? Did the transparent windows in our observation trap-nests disturb them more than other species we watched? Whatever possible reasons, the mating behavior of *T. vagulum* requires further study.

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